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Heritable Color Variants in *Automeris io* (Saturniidae)

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Abstract: *Automeris io* populations east of the Mississippi River and north of the Gulf States show extreme sexual dimorphism in forewing dorsal coloration. The yellow males are relatively uniform and the red-brown females are more polymorphic in appearance. A large number of inbred experimental lines has yielded several genetic color forms not known from wild sampling. The Mendelian heterozygote "broken-eye"/ "claw", the more polygenic "large" and "small" eyespot and the polygenic "broad" to "narrow" black intermarginal hindwing band genes were reported in 1978. To these are added three simple Mendelian recessives: dorsal hindwing "teardrop" with variable expressability; "brown" forewing dorsal ground color; and "rose" fore and hindwing ventral ground color, plus a recessive that produces "yellow" larvae when homozygous. Variability of wild males in Louisiana and wild females in Georgia is discussed.

Introduction

In 1964 a series of crosses were made within *Automeris io* (Fabricius) to determine the genetics of this species hindwing eyespot. Eyespot-like markings have evolved independently many times among insects, fishes, reptiles and birds. Very large eyespots may function as an escape mechanism, the possessor eluding capture by creating a "startling effect" on potential predators, enhanced by a variety of behavioral activities associated with the "eyes". Darwin (1859) was an early commentator on its survival value. Blest (1957) and Brower (1960) are among more recent investigators of eyespots on lepidoptera.

Automeris io, like many other members of its genus, has a large eyespot on each hindwing dorsum. The "eyes" of wild-caught moths are slightly variable in size. My initial experimentation was two phased: to increase the size of the hindwing eyespot by repeatedly crossing moths with the largest eyespots; and the second phase to reduce the eyespot by crossing moths with the smallest eyespots in successive generations. The results of these experiments not only revealed developmental genetics of the eyespot but by serendipity the several inbred lines exposed various remarkable Mendelian recessives altering the conspicuous markings of the moth (Manley 1978). The "broken-eye" breeding program was terminated in 1986 with the loss of the several lines, due to adverse weather conditions that summer. During the twenty years of continuous selective inbreeding, several additional variations of the conspicuous

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markings and ground color were produced. The genetics of eyespot size and of a hindwing/forewing pair of characters, "broken-eye" and "claw" was described and illustrated earlier (Manley 1978). In the present paper one more pattern variant "teardrop", two forewing ground color genes "brown" and "rose" and a larval color form are discussed and figured.

Materials and Methods

Breeding stock was derived from wild Pennsylvania *Automeris io* females taken in 1963 in the vicinity of Klingerstown, Schuylkill Co. First instar larvae were started in sleeves on wild Black Cherry (*Prunus serotina* Ehrh). Final instar larvae were placed in screened cages, with leaves available for cocoon spinning. Cocoons were refrigerated at 5°C from October to May. Pupae were placed in screened cages at room temperature in early May; adults emerged in early June. Adult behavior and breeding techniques have been described in detail elsewhere (Manley 1991). Crosses were made from selected individuals, and specimens involved in experimental crosses and their progeny were killed and spread for permanent reference. Virtually all specimens are deposited in the Entomology Division, Peabody Museum of Natural History, Yale University (YPM).

Description and Modifications of Conspicuous Wing Markings

The conspicuous markings (Fig. 1) are: dorsal hindwing eyespot, nor-

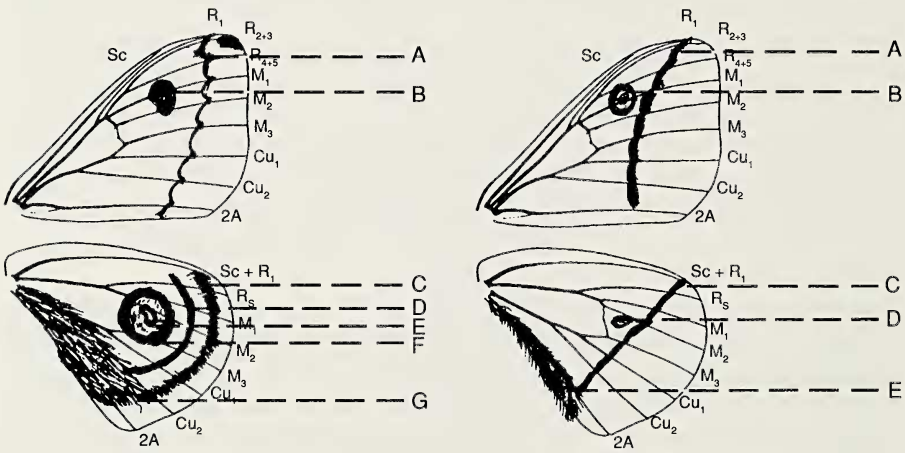

Fig. 1. Venation, color patterns, and conspicuous markings of *Automeris io io*. Dorsal surface: A - chevron line; B - forewing discal patch; C - outer marginal band; D - inner marginal band; E - focus or pupil of eyespot; F - eyespot; G - basal hair band. Ventral surface: A - forewing bar; B - discal patch; C - hindwing bar; D - hindwing discal spot; E - basal hair band.

mally round or oval, always black, with a gray or bluish iris surrounding the small white pupil or "focus" (Nijhout 1978, 1980, 1981) located in the center of the hindwing; the dorsal forewing discal patch, normally a kidney shaped mark slightly posterior to the costal region on the areolar area of the forewing, may extend along the subcostal and radial veins forming four blunt finger-like projections toward the outer margin of the wing; the ventral forewing discal spot, an oval patch of black scales with a small spherical white pupil or patch, commonly called the forewing ventral eyespot. The ventral hindwing discal spot is located beneath the white pupil or "focus" of the dorsal hindwing eyespot in the form of a white dot or "focus", it does not appear to be associated with the dorsal hindwing eyespot (Manley 1978). The other conspicuous character is the black intermarginal band which is genetically independent of the other conspicuous markings, its width controlled by a single gene which broadens the band.

Variant Imaginal Phenotypes

A. HINDWING DORSAL "TEARDROP"

In 1973 two inbred lines 11-70 and 13-70 expressing the "broken-eye" phenotype, produced a male and two females with a new variant eyespot having an anterior black satellite spot. Its emergence from the eyespot was reminiscent of a brimming tear, and was ultimately named "teardrop". The spot is usually connected to the eyespot but is sometimes entirely separated, especially if very small. There is a pronounced asymmetry in size and shape of the "teardrop" between the left and right wings. When it is present in an individual showing "broken-eye", it can easily be mistaken for another outreaching lobe, thus the "teardrop" variant was initially overlooked (Plate 1, Figures 1-6).

Again in 1974, six "teardrop" forms were noted in the 2100 adult *io* spread for study. Three more from a cross involving the normal eye, recessive to "broken-eye", were observed as small black spot separations from the black outer ring of the eyespot, suggesting the possible formation of a line breeding true for a normal eyespot plus a "satellite". The years 1975-1976 produced no variant eyespots in the "broken-eye" inbred lines, indicating an unstable developmental pathway due to inbreeding rather than a discrete "gene" controlling trait. In 1977 the 13-70 "broken-eye" inbred line produced a female with an eyespot variant which we then finally designated as "teardrop", and two other females had the "teardrop" variant superimposed over the "broken-eye", so that only a small portion of the "teardrop" extended beyond the "broken-eye" area. The 1978 "broken-eye", 13-70 series, produced 12 females and 6 males with evidence of the "teardrop" eyespot modification; five matings resulted in no fertile ova.

The "teardrop" variant was not observed again until 1982 when two crosses of the 13-70 inbred "broken-eye" line produced "teardrop" in 12 females and three males. A successful mating of a pair with "teardrop" eye initiated the "teardrop" line. A single cross of "teardrop" parents,

Plate I. Varying degrees of expression of "teardrop" eye in females of *Automeris io.*

Fig. 1. Cross 27-85 "teardrop" × teardrop Typical "teardrop" expression.
Fig. 2. Cross 4-73 "broken-eye" × "broken-eye" "Teardrop" expression from the recessive normal eye in the "broken-eye" line.
Fig. 3. Cross 5-74 "broken-eye" × "broken-eye" "Teardrop" expression with a "satellite" spot to the recessive normal eye in the "broken-eye" line.
Fig. 4. Normal eyespot, Wild Colorado female. Control.
Fig. 5. Cross 7-74 "broken-eye" × "broken-eye" "Teardrop" superimposed on "broken-eye".
Fig. 6. Cross 28-85 "teardrop" × "teardrop" Expression of incomplete penetration, note ellipsoid shape of eyespot.

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obtained in 1983 produced in 1984 two successful matings out of 15 attempts; 1985 provided enough "teardrop" adults to set up the entire range of experimental crosses, resulting in eight successful crosses out of 50 matings, which provided the necessary data to analyze phenotypes expressed by this condition. In 1986 two "teardrop" matings were successful, thus maintaining the genetic strain for further study. Crosses in 1987 produced four successful matings, but all larvae died due to adverse weather and line was lost.

The "teardrop" eyespot is controlled as a recessive (Fig. 2); as crosses to normal wild *A. io* produce no "teardrop" eyespots in the F 1 generation. In backcrosses, "teardrop" appears only if the normal-eye parent is heterozygous for the "teardrop" gene. Crosses of "teardrop" × "teardrop" all have "teardrop" or if no satellite spot is present, the form is an ellipsoid instead of a round eyespot. No precise frequencies of ellipsoid eyespots to

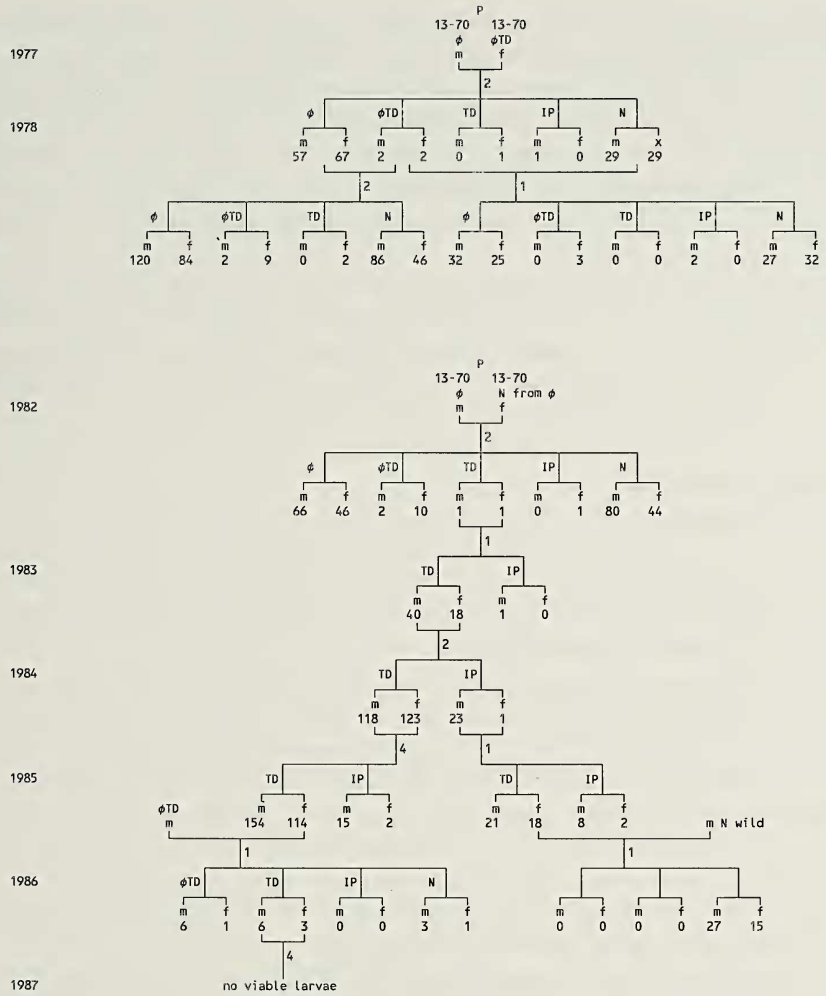

Figure 2. Isolation crosses from inbred 13-70 broken-eye line to establish pure lines of the "teardrop" phenotype in *Automeris io*. Numbers indicate the successful matings. Abbreviations: ø Broken-eye; TD Teardrop; IP Incomplete Penetration; N Normal Eyespot.

"teardrop" have been determined, due to the difficulty of evaluating the wide variation in expression of the ellipsoid eyespot. There seems to be a slightly greater ellipsoidal distortion in males than in females.

The "teardrop" gene has highly variable expressibility (Hartl 1980). It demonstrates a reduced or incomplete penetrance (Herskowitz 1980), some moths appearing normal for eyespot yet being homozygotes for the gene to express the "teardrop" phenotype. Crosses involving parents with normal appearing eyespots from the "teardrop" line produced the same phenotypic ratios as did parents possessing the "teardrop" eyespot.

Unlike the "broken-eye" gene, the "teardrop" gene appears to be independent of the forewing discal patch, as none of the 650 "teardrop" specimens studied show any distortion of the forewing discal patch. The fitness of "teardrop" broods were low due to their inability to mate, and to mortality of first instar larvae due mainly to their poor acceptance of a suitable food plant. When matings were successful, and first instar larvae fed well on *Prunus serotina*, then maturation and survival rate of pupae was normal for *A. io*.

Over much of its range, *Automeris io* has spectacular sexual dimorphism, due to the bright yellow forewings of males and the deep brown-red of many shades of the forewings of the females. It is interesting that the "teardrop," "broken-eye"/"claw," and eyespot size genes show no pronounced sexual differences.

B. GROUND COLORS

1. Basic description of ground color of *Automeris io io* wild type

Many authors have referred to the extreme variability of *Automeris io io* within any portion of its range. Numerous infraspecific forms, with many that are basically localized genetic variants, have been named (Packard 1914, Ferguson 1972).

A basic pattern emerges from controlled breeding experiments, the study of many wild specimens across its range, and mass samples from critical areas such as Florida, Georgia, Louisiana, Texas, New Mexico, Colorado, and northeastern United States. Deviations from this pattern have been isolated and genetically analyzed. The principal ones and some rare aberrations are discussed in this paper. The color descriptions of each sex, including noteworthy regional variations to the basic color pattern, are discussed. Specific regionally expressed genes changing the basic color pattern are genetically analyzed.

Emphasis is given only to ground color patterns as the genetics of the conspicuous markings typical to all *A. io io* and its subspecies is known (Manley 1978). Variation in ground color of the unique geographical subspecies of *A. io io* will be discussed in separate publications. Maerz and Paul 1930, color plate designations and descriptive terminology is used to describe color throughout the manuscript.

The ground color of males is jasmine or bright yellow. The dorsal forewing contains the kidney shaped forewing discal patch; the chevron line, parafocal elements (Schwanwitch, 1924; and Suffert, 1927) are located approximately two-thirds of the distance, beginning in the anal 2 cell and extends upward to the subcosta cell at the margin. The line is frequently broken in the radial cell area, in some cases absent or reduced to a small patch in the anal 2 - cubitus 2 area. The color of these markings is determined by a series of complementary genes whose expressions range from dull rosy red to opal grey.

The dorsal hindwing of the male is consistently yellow with a dense area of long rosy red scales, the basal hair band, extending from the point

of attachment of the wing to the metathoracic body segment. These hairlike scales cover the surface of the anal 2 and cubitus 2 cells and fuse with the outermarginal band. The outermarginal band is generally rosey red parallels the contour of the margin of wing beginning in the anal 2 cell extending to the subcostal + radial 1 cell of the wing. Its width acts independently of the highly conspicuous black intermarginal band, whose width is controlled by a single gene (Manley 1978).

The forewing ventral surface of the male is yellow. The forewing bar, a rosy red line of scales, separates the outer one-third of the wing. This line begins at the anal 2 cell and extends forward to the outer margin terminating in radial 1 or frequently in the radial 4+5 cell area. The inner two-thirds of the ventral forewing may be rosy red, the amount varies from a limited expression, resulting in a generally yellow forewing, to full expression with the rose color extending from anal 2 area to radial 4+5 vein. A yellow band along the outer margin covers the subcosta, Rl and R2+3 cells, its presence is enhanced when a full extension of the rosy coloration of the inner two-thirds of the wing is present.

The ventral hindwing is light yellow and is semi-transparent in that the conspicuous markings on the dorsal surface are visible, especially the focus of the eyespot which appears as a white dot. The size of the dot is dependent upon the size of the focus of the eyespot. The ventral hindwing bar is a line of rosy red scales extending from the marginal terminus of the radial 1 vein diagonally across the wing to the anal 2 cell separating the outer third of the wing. The bar may be a fine line or quite broad and distinct. A fine band of rosy red scales extends along the outer margin of the hindwing.

2. Regional differences in ground color in Georgia and Lousiana

Regional modifications of the basic ground color are most easily recognized in the males which have yellow forewings, less observable in females which have dark forewings. Along the southern boundary of *A. io io* where it is bivoltine (Manley 1991), the ground color is subject to a variety of regional gene modifications. Those in northern Georgia are particularly dramatic, as a high degree of uniformity is expressed in individual broods reared from wild females. A seasonal polyphenism (Shapiro 1984) appears to exist in that several broods may differ phenotypically from each other, a situation not observable in the wild due to the natural dispersal of the brood. Dr. Hermann Flaschka of Decatur, DeKalb County, Georgia, has over the past seven years, supplied ova from wild females, which have produced the "yellow larva" phenotype and some large broods with uniform ground color expressions not typical of northern *A. io io*. In several of these broods the males were uniformly orange-yellow ground color, Plate 2, Figure 3; females of these broods were predominantly copper brown, suggesting a high degree of homozygosity or independent of a sexual dimorphism mechanism for ground color. The male progeny of one wild female were predominantly honey

yellow, Plate 2, Figure 10, with some typical yellow males. These copper or yellow brown males show no close similarity to the tawny orange brown males of the *Automeris io lilith* from along the Georgia coast and the Florida peninsula. The status of *A. io lilith* in Florida will be discussed in a later paper.

In Louisiana there must be a wide range of genes which make *A. io io* males diverse in their color patterns. Phenotypes for some of these modifications are present in northern *A. io io* but not expressed to the degree observed in Louisiana, except in controlled inbred lines described later in this paper. Vernon A. Brou collected over an eight year period (1978-1985) more than eight hundred *Automeris* males in Abita Springs (St. Tammany Parish), Edgard (St. John's Parish), and Weyanoke (West Filiciana Parish). A ground color phenotype not observed in our 25 years of breeding northern *A. io io* has rosy or brown scales on the ventral wing surface of these males, and on the limited number of females we have studied. It was present in 92% of the Louisiana sample. Unique to this phenotype is its intensity of expression, which appears to be influence other genes producing a "brown wing" phenotype. Manley (1978) demonstrated that there was no relationship of the dorsal surface genes for conspicuous markings to those on the ventral surface. Enhancement of the dorsal surface "brown wing" phenotype intensifies the expression of rosy or brown scales on the ventral wing surface.

Another ground color phenotype observed in the Louisiana sample is rose-brown or cinnamon, Plate 2, Figure 9, forewing ground color gene, observed in six percent of the males in the March-June diapausing generation. This color pattern was not expressed in the non-diapausing generation flying July-September. The mechanism of expression of this gene appears to be similar to the one controlling the tawny-brown males of the diapausing generation of Florida *A. io lilith*. This color pattern has not appeared in our 25 years of inbreeding Pennsylvania *A. io io*. Pupae from southern Louisiana, finally obtained fall 1989 should allow us to further evaluate this phenotype and others unique to that region, especially since there should be females for study.

The female ground color of *A. io* is difficult to describe due to the wide array of potential hues that range from red to opal grey. The ground color pattern is sex limited (Remington, 1954, 1976) and is further complicated by the expressions of specific genes, conspicuous in males but masked by ground color or absent in expression in the female. Plate 3, Figures 19-30 show females representing the potential range of ground colors observed in *A. io*. Wild specimens were used to demonstrate the predominant color of the female displayed in various regions of its range. Pennsylvania *A. io* has in its genome the ability to produce any of the basic ground colors found in the United States, with the exception of the tawny brown male coloration of the diapausing generation of Florida *A. io lilith*. The source of genes for this color pattern will be presented in a separate paper on the status of the Florida populations.

The color range of the dorsal forewing, based on examination of over 5,000 female specimens, is red tones in the range of Persimmon or copper brown, Plate 3, Figure 19; the darkest tone is opal grey, Plate 3, Figure 30. The dorsal forewing discal patch may be slightly darker than the basic ground color or it may blend into the ground color pattern; it is not as conspicuous as it is in males. The chevron line separating the outer third of the wing may be prominent or it may blend into the ground color. Occasionally the outer margin of the wing will be lighter in color, making these females more conspicuous.

Figures 20 through 28 represent the most frequently expressed forewing ground colors of *A. io io* in the United States. In controlled crosses a majority of females have similar color patterns with a strong tendency toward dull plum red tones suggesting the expression of a heterozygous complementary gene complex for color. Many predominantly rosy red to plum red female crosses produce a small number of darker forms, suggesting that opal gray is recessive.

The subdued color tones of the dorsal forewing of a wild female may make it inconspicuous when resting in the shadows of leaves near the trunk of a tree.

The dorsal hindwing color pattern is uniform throughout the species range; it forms the background for the display of the conspicuous "eye" markings. With the exception of the three narrow marginal bands the central portion of the hindwing is always a shade of yellow. The black eyespot and black intermarginal band are displayed in the yellow area. The band along the margin of the wing may be a fine line, or a narrow

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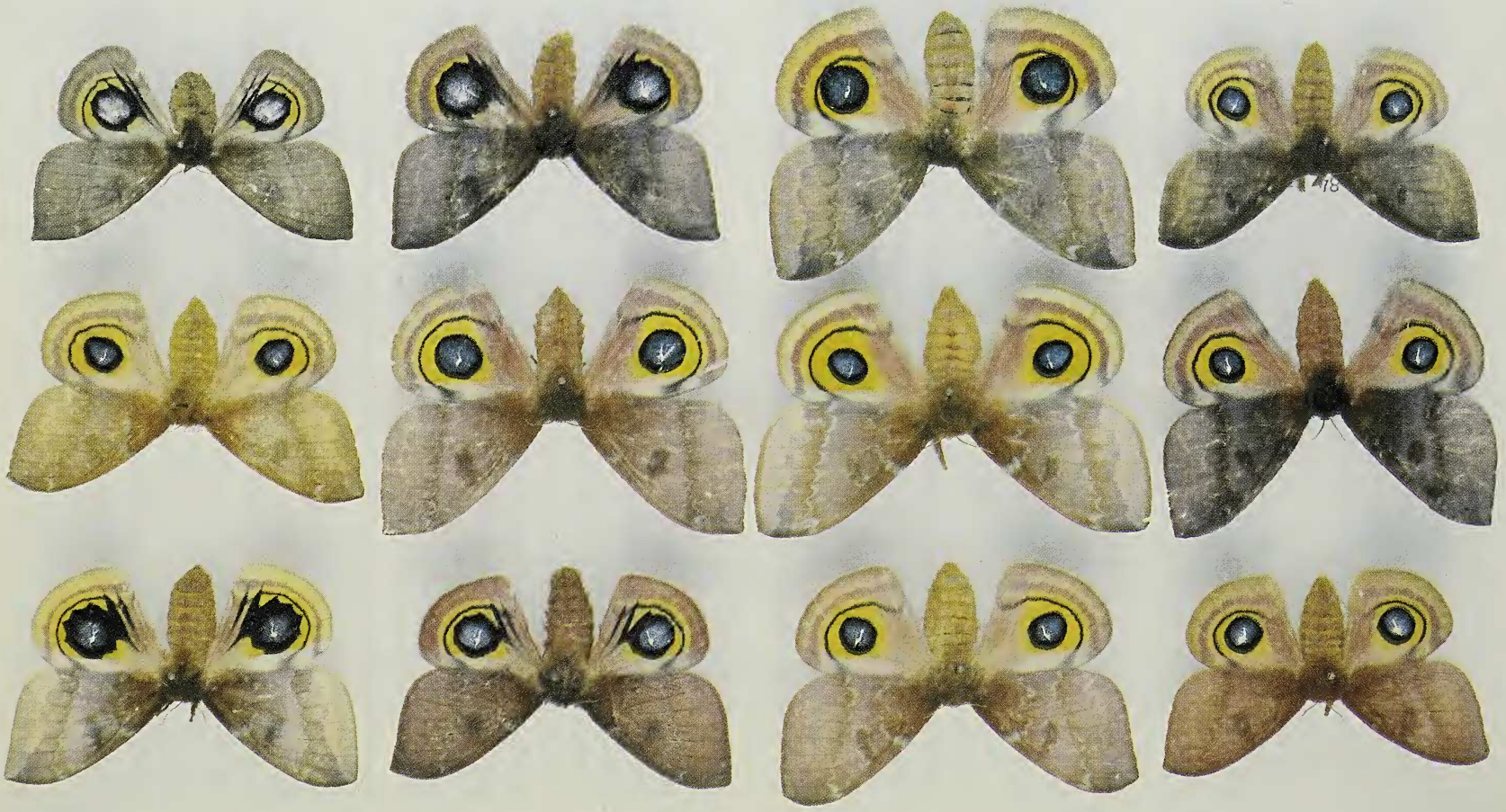
Plate 2. Color range of *Automeris io* males and digress of expression of the rose underwing phenotype.

Fig. 7. Wild Liverpool Pennsylvania, representing typical ground color for northeastern Io males.
Fig. 8. Progeny of Wild Georgia female — orange red ground color phenotype assumed to be homozygous as all siblings were same color.
Fig. 9. Louisiana male, phenotype observed only in the diapausing generation.
Fig. 10. Wild northern Georgia honey-brown phenotype.
Fig. 11. Cross 9-74. Full expression of "brown" wing gene.
Fig. 12. Wild Louisiana, partial expression of "brown" wing gene, usually present in varying degrees in Louisiana males.
Fig. 13. Cross 7-73. Tawny pink northern male, color occasionally appears in Northern Io.
Fig. 14. Cross 30-85. "teardrop" × "teardrop". Typical "teardrop" male.
Fig. 15. Cross 9-74. Full expression (YyRR) of rose underwing phenotype on fore and hindwings.
Fig. 16. Cross 10-85. Partial expression (yyRr) of rose underwing phenotype hindwing rose, forewing normal.
Fig. 17. Cross 10-85. Limited hindwing expression (YyRr) of the rose underwing phenotype rose dusting on hindwing.
Fig. 18. Cross 10-85. Normal (YYrr) hindwing ground color.



band of color identical to the basic ground color of the dorsal forewing. The middle band is always lighter in color, a suffusion of the ground color scales on yellow, and its width varies. The outer marginal band bordering the yellow area of the dorsal hindwing is generally the widest and most pronounced. It may be the same color as the forewing blending the hindwing profile with the forewing, or it may be brighter colored and quite conspicuous. Extending from the base of the wing along the inner marginal surface, area Cu2 and 2A, is the basal hairband, a dense patch of long hairlike scales ranging from rosy red to opal grey. The color of these scales blends with the ground color of the forewing regardless of the depth of color of the forewing.

The ventral surface is uniformly colored, both forewing and hindwing. The colors are slightly lighter and duller than those of the dorsal surface. As in the male, a line of rosy red or plum red, rarely opal grey, scales forming the dorsal and ventral hindwing bars separate the outer one-third of the wing. The bar is a line of deeper colored scales extending from the middle of the anal 2 upward across the wing to the terminal point of the radial 1 or radial 4-5 vein on the margin of the ventral forewing surface. The bar extends from the anal 2 cell upward to the point where the subcosta + radial 1 or radial 5 vein terminate on the margin of ventral hindwing. Occasionally bars are missing or masked by certain genes, namely the red underwing gene, making the ventral surface a single color.

The ventral forewing discal spot, an oval or egg shaped patch of varying size of black scales with a small white pupil or focus, is the conspicuous marking on the ventral surface. The gene controlling its size and intensity is independent of genes controlling conspicuous markings on the dorsal surface (Manley 1978). The white pupil of the eyespot on the dorsal hindwing is visible ventrally as a white dot in the center of the hindwing.

Plate 3. Color range of *Automeris io* females.

Fig. 19. Progeny of Wild Georgia Female, sibling Figure 8 male, homozygous dominant red.
Fig. 20. Wild New Jersey.
Fig. 21. Cross 9-72. Female shows "broken-eye".
Fig. 22. Cross 14-73. Female shows full expression of "broken-eye".
Fig. 23. Wild Louisiana.
Fig. 24. Wild Colorado.
Fig. 25. Wild Pennsylvania.
Fig. 26. Wild New Jersey.
Fig. 27. Wild Kansas.
Fig. 28. Wild Georgia.
Fig. 29. Cross 9-73. With full expression of "broken-eye".
Fig. 30. Cross 3-74. Homozygous recessive for plum gene, a rare expression.

3. "Brown" forewing dorsum

Any mass sample of eastern *A. io io* will have a high frequency of males with brown scales of varying intensity on the dorsal forewing. Our Liverpool, Snyder County, Pennsylvania sample (N=123) taken over a 25 year period shows 69% of the males with some degree of brown suffusion. *A. io* in the Peabody Museum Collection at Yale University and other large mass samples show a similar percentage of expression of this phenotype. In most cases the genes for "brown" wing are minimally expressed in wild males; however, strong expression of the genome can quickly be produced by selective breeding. With the maximum expression of this gene complex, the color of the basal two-thirds of the dorsal forewing may be rosy red to brownish opal grey depending on the basic ground color gene complex being expressed. "Brown" wing is not observable in females as it may be masked by the normal dark ground color (or perhaps it is not present in females).

The initial full expression of "brown wing" gene complex was first observed in cross 15-71, F5 generation of the inbred line for "broken-eye" (Plate 2, Figure 11). Crosses were made yearly 1972-1978 in an attempt to isolate true breeding lines of "rosy red" and "opal grey". Color isolation was abandoned in 1978 due to the inability to diagnose the phenotypes of the females, and the relatively high percentage of uniform brownish males present in every cross. Females in these crosses were uniform in ground color.

Males, assumed to be homozygous, having full expression of maximum forewing coloration, were mated with sibling females with background colors, predominantly "rosy red" or "opal grey", produced a relatively uniform distribution of male color patterns regardless of the ground color of the male, suggesting a sex-limited polygenic autosome controlling its expression. Frequency of the full expression of the gene in these crosses averaged 33.8%.

The Louisiana *A. io* population differs from others in that random mass samples show the full range of expression of the "brown" wing phenotype, making it distinct from other *A. io*. A random mass sample (N=805) segregated: "evidence" 21.1%; "medium expression" 42.3%; "strong expression" 33.2%; "no expression", yellow wings .03% for the "brown" wing gene. Although the full expression of the gene was .07% by wild random mating it provides evidence this gene plays a major role in the unique color patterns of Louisiana *A. io*. The similarity in male color patterns between controlled crosses of northern *A. io* and random wild matings in Louisiana involving the "brown" wing gene make their separate identities difficult.

4. "Rose" underside phenotype

The rosy underside phenotype, Plate 2, Figures 15-16-17, conspicuous in the yellow male, is extremely difficult to observe in females whose normal rose ground color masks its degree of expression. Analysis of this

quantitatively expressed recessive is further complicated by the (difficulty in selecting females with a recognizable degree of expression of the gene to mate with "rosy" underside males. Evidence of the phenotype first appeared in cross 18-69 and F 3 inbred line for "broken-eye" gene when 17 males possessed "rosy" scales of varying density superimposed among the normal lemon yellow scales that form the basic underwing ground color.

This phenotype was expressed regularly in the 13-70 inbred line for "broken-eye" from 1971-1975. A 1975 cross produced individuals with the entire ventral surface deep rose, Plate 2, Figure 15; this phenotype was present in varying degrees of expression, on approximately 50% of the males, suggesting a 1:1 ratio of yellow to "rosy" underside for that cross. Serious attempts to isolate the underlying gene or genes began in 1981 and continued through 1985. To measure the degree of expression, the rosy phenotype was designated as; "normal yellow" (YYrr); "trace", a faint dusting of rosy scales along the outer margin of the hindwing and faint dusting on the hindwing venter (YYRr); "rose dusting", a light to medium rose dusting over the entire hindwing surface (YyRr); and "deep rose", heavy rose scales on the ventral hindwing (yyRr); and in extreme instances heavy rose scales extending over the entire ventral forewing (yyRR).

By combining the phenotypes of six crosses for "rose" underside using the above segregation criteria, phenotypes of the offspring were 229 yellow, 77 "rose trace", 89 "faint to moderate dusting" and 28 "heavy rose dusting", a close fit to a 9:3:3:1 ratio ($x2=1.6$, $df=2$, $p>.50$). On rare occasions when the recessive opal gray ground color is expressed, the "rose" underside genome is expressed as grayish brown (N=4:423). I have never observed this phenotype in wild males in northeastern United States; however evidence of this phenotype was observed in 0.5% of the Louisiana males (N=805).

5. "Yellow larvae" gene

Ova from a female taken in DeKalb County, Georgia produced two distinctly different larval colors: the normal green and lemon yellow in a 123:97 ratio. During my 25 years of *A. io* breeding no "yellow larvae" had been observed.

The occurrence of mutations affecting the color of the hemolymph of Lepidoptera is well documented. Certain rare variations in larval color were first reported by Gerould (1921) blue-green vs. green in *Colias philodice philodice* Latreille in New Hampshire; Hoffman and Watt (1953) described blue-green vs. green in *Colias philodice eriphyle* Edwards in Colorado; Gray (1953) reported yellow vs. green in *Pieris rapae* L.; Stehr (1953) recorded yellow vs. green larvae in moths of the genus *Chorestoneura*; and Collins and Weast (1961) bluish vs. green larvae (1:20) in *Automeris io texana* Barnes and Benjamin.

"Yellow larvae" were separated from "green larvae" into screen cages

during final instar. Rearing continued on native wild cherry (*Prunus serotina* Ehrh.) and daily observations were made to note any differences in behavior and growth. None was observed. Unique to this brood was that the "yellow larvae" attracted large numbers of *Arilus cristatus* L. the reduviid Wheel Bug.

These large insects could project their long beak through openings in the screen into the body of larvae crawling along the surface. Although some "green larvae" were killed by Wheel Bugs, they seem to, reason unknown, concentrate on the more conspicuous "yellow larvae". A mass sample of 87 *Arilus* was taken in the vicinity of the cages, few have been observed in the area since that time. Gerould (1921-1926) observed that English Sparrows (*Passer domesticus* L.) could locate and feed on the highly visible "blue-green" larvae of *Colias philodice* while missing the normal green larvae.

Surviving larvae began spinning cocoons on 1 September, and pupation was complete on 12 September 1985. There was no observable difference in shape or color of cocoons, pupae were stored at 5°C in plastic containers from October to 1 May 1986. Pupae were placed in hatching cages and a temperature of approximately 22°C was maintained until adults emerged. Ninety-seven "yellow larvae" produced 49 pupae; their emergence period was 1 June - 23 June; sex ratio of adults, males 15/females 0. One hundred twenty three "green larvae" produced 71 pupae; their emergence period 1 June - 29 June; sex ratio of adults, males 30/females 5. Sixty-five pupae eventually died, sexed by pupal case size; "yellow larvae", males 25/females 9; "green larvae", males 18/females 13. The high loss of pupae could be attributed to early September pupal formation resulting in many pupae lacking the ability to diapause. Non-diapausing pupae normally hatch in October, thus are incapable of enduring extended periods of storage at 5°C Manley (1991). The adult males are identical in color regardless of larval color. Three matings of "yellow larvae" males to "green larvae" females produced no fertile ova and the brood was lost.

Fall 1988 Dr. Flaschka sent pupae reared from a wild female taken 24 June 1988 in the vicinity of Lake Allatoona, Bartow County, Georgia which had both "yellow" and "green larvae". Larvae were separated by color during the final instar to enable one to isolate adults for future study. From this mating only "yellow larvae" males survived. Females from "yellow larvae" apparently were not able to develop into pupae; as shrivelled, spine-covered larval bodies were found in the cocoons they had spun. "Green larvae" developed normally, permitting a successful mating of a "yellow larva" male and "green larva" female. Larvae of this cross were poor feeders and were small sized in the final instar in comparison with other crosses. Pupae from this mating produced ten green larva males, one yellow larva male, two green larva females and no yellow larva females. This brood produced no successful matings.

The apparent 1:1 ratio (123 "green" to 97 "yellow" larvae) of the DeKalb

County, Georgia female in 1985 suggests that "yellow larvae" is expressed as a recessive. A female, heterozygous for "green larvae" mated with a homozygous recessive "yellow larvae" male. The Barton County, Georgia female (1988) apparently had the same genotype suggesting the necessity of the presence of at least one dominant allele for "green larva" color for females to survive, as no homozygous "yellow larva" females have survived to date in this study.

The *Automeris io* research team (Manley 1991) was alerted to watch for "yellow larvae" in wild populations in the Gulf Coast states. David Ritland found a wild brood of Io on wild cherry with "yellow larvae" in Chattahoochee National Forest, Union County, Georgia, which he reared to adults. His comment: "Yellow larvae were very yellow, with no hint of green. There were no intermediate colored larvae" (Ritland 1986). It would appear the "yellow larva" gene is widely distributed across northern Georgia. The other report of wild "yellow larvae" comes from Terhune S. Dickel, who collects extensively in the Florida Keys. He wrote in 1986: "All Io larvae that I have seen in southern Florida and the Keys thus far have been bright lemon-green." Lemon-green larval color in southern Florida was initially observed by Annie T. Slosson in 1887 (Beutenmuller, 1895).

To date these are the only areas in the southeastern United States where "yellow larvae" of *A. io* have been observed.

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